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THE GENERA OF NYCTAGINACEAE IN THE SOUTHEASTERN UNITED STATES[1]

A. LINN BOGLE

NYCTAGINACEAE A. L. de Jussieu, Gen. Pl. 90, 1789, "Nyctagines," nom. cons.

(FOUR-O'CLOCK FAMILY)

Annual or perennial herbs, sometimes scandent shrubs, or trees; stems procumbent to erect, sometimes climbing by means of stout recurved thorns; roots fibrous or fleshy to tuberous; leaves mostly opposite, exstipulate, simple, entire, equal or unequal, sessile or petiolate, membranaceous or fleshy, glabrous or pubescent; inflorescence terminal or lateral, cymose [or racemose], diffuse or congested, bracteate, the bracts sometimes large and bright colored, either free or united in an involucre around one or more flowers and sometimes simulating a calyx [or flowers axillary and solitary]; flowers incomplete, perfect or imperfect (the plants monoecious or dioecious), showy or inconspicuous; perianth uniseriate, usually pen-

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tamerous, of five fused sepals, the calyx small, fleshy and inconspicuous to large, membranaceous, petaloid and colorful, simulating a corolla; aestivation induplicate-valvate (plicate or contorted); corolla none; stamens one to many, hypogynous, filaments filiform, unequal, free or united basally in a shallow collar, the anthers small, tetrasporangiate, 2-loculate at maturity, dehiscing by longitudinal slits; carpel one, ovary superior, unilocular, ovule solitary, basal, hemianatropous to anacampylotropous, integuments 1 or 2; style long filiform; stigma capitate to penicillate. Fruit an achene or utricle inclosed within the persistent fleshy (berry-like) to hard and leathery glabrous or pubescent, often 5(–10) ribbed base of the perianth tube, the ribs often viscid glandular or bearing stalked capitate glands; seed solitary, the seed coat membranaceous; embryo straight or curved, cotyledons foliaceous, endosperm sparse, perisperm abundant. TYPE GENUS: *Nyctago* A. L. de Jussieu, nom. illegit. = *Mirabilis* L.

A family of about 26 (to 30) genera, containing about 300 species distributed primarily in the tropical and subtropical regions of the New World, and represented in our area by about 14 species of four indigenous genera (*Boerhavia* L., *Mirabilis* L., *Okenia* Schlechtend. & Cham., *Pisonia* L.). In contrast, about 19 species of four genera (*Boerhavia*, *Bougainvillea* Commerson, *Mirabilis*, *Pisonia*) occur in Malaysia, but only *Pisonia* among these is unquestionably native to southeastern Asia (Stemmerik). *Boerhavia* is a pantropical weed. Several species of *Bougainvillea* are widely cultivated as ornamentals in the tropics, and *Mirabilis Jalapa* L. has escaped from cultivation in many tropical areas.

The systematics of the family are problematical, there being no consensus as to either the number of tribes represented or the number or circumscription of some of the larger and more important genera (e.g., *Mirabilis* sensu lato, *Pisonia* sensu lato). The genera have been disposed in four subfamilies (Fiedler) or tribes (Heimerl, 1889) or, more recently, in five tribes (Heimerl, 1934; Eckardt), or eight tribes (Hutchinson). Standley (1918), considering only the genera of North America, recognized six tribes. Depending upon the system consulted, two (Heimerl) or three (Hutchinson) tribes are represented by the four genera indigenous to our area.

The tribe Nyctagineae (Mirabileae Meissner),[2] taken in the broad

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[2] A nomenclatural problem concerning the correct name of the tribe and subtribe containing the type genus of this family occurs because of a conflict in the wording of Article 19 of the International Code of Botanical Nomenclature in both the 1966 and 1972 editions, neither of which makes clear whether these names should be Nyctagineae and Nyctagininae or Mirabileae and Mirabilinae. In the 1966 edition, two criteria are given for the names of taxa below the level of family and above that of genus: 1) such names are formed by adding the appropriate suffix to the stem of a *legitimate name* of an included genus, and 2) "the name of any taxon of a rank below family and above genus which includes the type of the next higher taxon must be based on the *same stem as the name of the next higher taxon* . . ." (italics mine). In the 1972 version, the first criterion is retained, and the second is modified so that "the name of any taxon of a rank below family and above genus which *includes the*

sense of Heimerl (1934) and of Eckardt, is characterized by generally herbaceous to shrubby habit, mostly perfect flowers, the fruit inclosed in the persistent base of the calyx tube, and more or less folded or hooked embryos. Four subtribes are recognized in the Nyctagineae, of which subtribe Nyctagininae (Boerhaviinae)[2] is the largest (13 genera) and the only subtribe represented in our area by indigenous genera (*Boerhavia*, *Mirabilis*, *Okenia*). The other three subtribes are all monogeneric (Abroniinae, *Abronia*; Bougainvilleinae, *Bougainvillea*; Phaeoptilinae, *Phaeoptilum*). The genera *Abronia* and *Bougainvillea* are cultivated as ornamental plants in our area, but have apparently not become naturalized. *Phaeoptilum* Radlk. is an endemic of Angola and Southwest Africa.

The tribe Pisonieae Meissner, containing six genera but consisting principally of *Pisonia* L. and *Neea* Ruiz & Pavón, is characterized by trees or woody shrubs with mostly imperfect flowers; accessory fruits, the accrescent calyx base inclosing the utricle or achene; and straight embryos. Only *Pisonia* is found in our area. *Neea* occurs in South and Central America, approaching our area in the islands of the Caribbean.

The three remaining tribes of the family are small. Tribe Colignonieae Standley contains only the genus *Colignonia* Endl., with about eleven species in the South American Andes. Tribe Boldoeae Heimerl contains only the monotypic genus *Boldoa* Cav. of Mexico and Central America, while tribe Leucastereae Bentham & Hooker consists of four monotypic South American genera (*Andradea* Allemão, *Leucaster* Choisy, *Ramisia* Baillon, *Reichenbachia* Sprengel).

The relationships of the Nyctaginaceae are recognized by most authors

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type genus of the correct name of the family to which it is assigned is to be based on the *name of that genus* . . ." (italics again mine). Under either version of the Code these two criteria come into conflict in the case of any of the dozen conserved family names that are based on an illegitimate generic name (e.g., Caryophyllaceae, Nyctaginaceae, Sapotaceae). Under Article 18, Note 1, these conserved family names are both valid and legitimate, but Article 19 does not deal with the conflict noted above.

Nowicke (1970) was aware of this problem and, following the 1966 edition of the code then applicable, emphasized the second criterion, the name of the next higher taxon, concluding that "the tribe Mirabileae, subtribe Boerhaaviinae, which contains this genus *Mirabilis*, must become the tribe Nyctagineae, subtribe Nyctagininae." If the second criterion is to be used, Nowicke's names would also stand under the changed wording of the 1972 Code, in which "the same stem as the name of the next higher taxon" is replaced by the stem of the name of the type genus (*Nyctago*). But the first criterion of both versions of the Article, requiring the stem of a legitimate name of an included genus, is not met, since conservation of the family name Nyctaginaceae with *Nyctago* as the type genus does not validate the illegitimate name *Nyctago* Juss. It can, therefore, be argued that *Mirabilis* L. remains the legitimate name and stem for the designation of higher taxa, which then become tribe Mirabileae and subtribe Mirabilinae.

Since it is clear that the intent of the Code is to indicate the subfamily, tribe, and subtribe that include the type genus of the family name, Nowicke's decision to follow the second interpretation is adopted here, even though Nyctagineae and Nyctagininae are based upon an illegitimate generic name. It is desirable, however, that Article 19 be studied and amended to account for this problem in the Nyctaginaceae and other families, the names of which are conserved but are based on illegitimate generic names.

to lie among the families of the order Centrospermae (Bentham & Hooker, 1880; Heimerl, 1889, 1934; Standley, 1909, 1918; Eckardt, 1964), or more recently the Caryophyllales (Buxbaum, 1961; Cronquist, 1968; Takhtajan, 1969), where they are considered either to be derived directly from the primitive phytolaccaceous stock or to be in an unclear position (Buxbaum). With this group of families the Nyctaginaceae share several distinctive characteristics, including the presence of betalains rather than anthocyanins (Hegnauer, 1969), the frequent occurrence of anomalous secondary growth, the basal placentation of the ovule, and a constellation of embryological characteristics unique to the order (Cronquist, 1968). Hutchinson (1920, 1967) placed the family in his order Thymelaeales after the Thymelaeaceae ("for want of a better position") on the basis of the apetalous flowers and increasingly woody habit among the genera of Nyctaginaceae. This position was supported by Venkateswarlu (1948) on the basis of embryological evidence from *Pisonia aculeata*, but the bulk of morphological and anatomical evidence favors affinity with the Caryophyllales. Physiological evidence also supports this affinity, since Kendrick & Hillman have demonstrated in *Mirabilis Jalapa* L. and other species of Centrospermae the absence of a dark reaction which converts the far-red absorbing form of phytochrome to the red absorbing form. The presence of such a reaction is typical of other dicotyledons, but is lacking in monocotyledons, and its absence in these species is seen as a further suggestion of common physiology and ancestry between the Centrospermae and monocotyledons.

The Nyctaginaceae are distinguished from the closely related Phytolaccaceae by their usually opposite leaves, mostly cymose inflorescences, synsepalous and often corolla-like calyces that are plicate or contorted in the bud, solitary uniovulate carpel, and fruit an achene inclosed in the accrescent calyx base.

Gametic and somatic chromosome counts reported in the literature indicate diploid numbers of $2n = 92$, ca. 92, ca. 88–92 in *Abronia*; $2n =$ ca. 58 in *Allionia*; $2n = 26$, 42, and 116 in *Boerhavia*; $2n = 20$, 34, 51 in *Bougainvillea*; $2n =$ ca. 40 in *Commicarpus* Standley; and $2n = 52$, 58, ca. 58 in *Mirabilis* (incl. *Oxybaphus*). Counts are apparently lacking for *Okenia*, *Pisonia*, and other North American genera.

Several unusual floral modifications occur in the family. The flowers are apetalous and the calyx is inconspicuous in many genera, but in *Mirabilis Jalapa* and *Okenia* the calyx tube is large and colorful, simulating a corolla, while several involucral bracts form an apparent calyx. In *Bougainvillea* three large, brightly colored petaloid involucral bracts surround a cluster of flowers with relatively small and inconspicuous calyx tubes. The extremely sticky fruits of some *Pisonia* species are disseminated by adherence to the feathers of birds, while the fruits of *Okenia* are geocarpic, being pushed underground by their elongating pedicels.

Joshi & Rao found basic similarities in the floral plan and vasculature of *Boerhavia diffusa*, *B. repanda*, *Bougainvillea spectabilis*, and *Mirabilis Jalapa*. In *Bougainvillea* the perianth receives many traces from both the inner and outer rings of primary bundles in the pedicel; but in *Boerhavia* and *Mirabilis* only the inner ring of pedicellar bundles contributes to the perianth, providing ten traces in two cycles of five each in *B. repanda* and *M. Jalapa*, but only a single cycle of five traces in *B. diffusa*. Reduction in the number of stamens is accompanied by reduction in the number of traces to the androecium, from seven or eight in two cycles (*Bougainvillea*) to five or fewer traces in one cycle (*Boerhavia, Mirabilis*). Gynoecial structure is stated to be similar to that of *Rivina* L., of the Phytolaccaceae, and unlike that of the Thymelaeaceae, as exemplified by *Stellera* L. Joshi & Rao conclude that the ancestral nyctaginaceous flower had a perianth supplied by 10 traces in two cycles, two whorls of stamens, and a single carpel. They propose relationships to the Phytolaccaceae, as opposed to the Thymelaeaceae, despite resemblances in perianth form to the latter.

The term "anthocarp" has been used traditionally in connection with the Nyctaginaceae to designate the combination of the fruit (an achene or utricle) and the persistent, accrescent, hard, leathery, or fleshy base of the calyx tube that incloses it. There is, however, considerable confusion in the use of the term. Some authors say that there is a union between the perianth base or receptacle and the fruit, although, as will be seen in FIGURES 1–5, this is not the case in Nyctaginaceae. Jackson (Glossary Bot. Terms, ed. 4. 1928) defined an anthocarp as "a fruit formed by the union of the floral organs or part of them, with the fruit itself, as in the Nyctaginaceae." Similarly Munz & Keck (Calif. Fl. 1577. 1959) and Correll & Johnston (Man. Vasc. Pl. Texas 1746. 1970) say that an anthocarp is "a structure in which the fruit proper is united with the perianth or receptacle." Henderson & Henderson (Dict. Biol. Terms, ed. 8. 1963) define anthocarp as "a collective or aggregated fruit formed from an entire inflorescence, . . ." and both Jackson and Featherly (Taxonomic Terminol. Higher Pls. 1954) write that anthocarpous is said of "fruits with accessories, sometimes termed pseudocarps, as the strawberry and pineapple."

Asa Gray took perhaps the most general view of the anthocarpous fruit (Structural Botany, 300, 301. 1879). He wrote, "Accessory or Anthocarpous Fruits are those of which some conspicuous portion of the fructification neither belongs to the pistil nor is organically united with it, except by a common insertion. The part thus imitating a fruit, while it is really no part of the pericarp, is sometimes called a Pseudocarp. This condition may occur in either simple, in aggregate, or in multiple fruits." After giving the fruits of *Gaultheria procumbens* and *Shepherdia* [*canadensis*] as examples of simple anthocarpous fruits he added, "So, also, the apparent achenium or nut of Mirabilis, or Four-o'clock, and of its allies, is the thickened and indurated base of the tube of a free calyx, which contracts at the apex and encloses the true pericarp (a utricle or thin akene), but does not cohere with it."

In view of the multiple ways in which the term is used, the use of "anthocarp" in the Nyctaginaceae hardly seems worth continuing, particularly since some of the definitions incorrectly include union of the accrescent calyx base and the fruit. It seems better, although more wordy, to refer to the components of the accessory fruit of members of this family as the accrescent calyx base that incloses the fruit, which is itself an achene or utricle. (In this connection it should be added that Buxbaum interprets the structure in *Mirabilis Jalapa* that most workers have called the perianth or calyx base as being axial in nature, forming a hypanthium around the ovary and fruit, and bearing the corolla-like calyx at its summit.)

Embryological studies by numerous workers on several of the common genera and species indicate 4-sporangiate anthers and pollen grains that usually are 3-celled (rarely 2-celled) at anthesis. Ovules are crassinucellar and unitegmic (*Abronia, Boerhavia, Mirabilis*) or bitegmic (*Bougainvillea, Oxybaphus, Pisonia*), with the inner integument forming the micropyle. Endosperm formation is nuclear, becoming mostly cellular except at the chalazal end of the curved embryo sac. Development of the embryo is of the Asterad type (Davis, Schnarf).

The form and development of the fruits, seeds, embryos, and seedlings of 14 species of six genera have been described in detail in the extensive comparative surveys of Lubbock and Martin. In *Abronia* one cotyledon is abortive, resulting in a "monocotyledonous" embryo.

Recent comprehensive light microscope and scanning electron microscope studies of nyctaginaceous pollen morphology (Nowicke; Nowicke & Luikart) reveal a broad range of variation in such characteristics as pollen size (22–210 micra in diameter), shape (commonly spheroidal but with some prolate and oblate types, aperture form (variously 3–18-colpate or 12 or more pantoporate, the pores frequently operculate), and exine sculpturing (either spinulose and tubuliferous, the spinules varying in size and distribution, or coarsely reticulate with modification in the ornamentation of the muri and lumina). Sexine pattern is seen as a more significant characteristic than aperture pattern in establishing systematic relationships, and a correlation between pollen morphology and various selective pressures (xeric conditions, pollination vectors, stigma types) is suggested. Nowicke (1971) suggests that this correlation of form with ecological conditions may possibly be demonstrated in the subtribe Nyctagininae, which contains thirteen genera (sensu stricto) of plants of warm, dry habitats, the pollen grains of which are characterized by thickened walls and small, frequently sunken, operculate pores. Nowicke's evidence supports the integrity of the tribal and subtribal delimitations of Heimerl (1934), but pollen morphology within the large subtribe Nyctagininae (Boerhaviinae) is relatively uniform and of very limited value at the generic level.

Stem and root anatomy in the few genera of Nyctaginaceae that have been studied (*Boerhavia, Bougainvillea, Heimerliodendron, Mirabilis*) is anomalous in that: 1) the primary vascular bundles are scattered in the ground tissue, rather than being arranged in a cylinder, and show very limited secondary growth; and 2), secondary thickening is due to a single, permanently acting, extra-fascicular meristematic zone of cortical origin, termed the primary thickening meristem. The latter produces anomalous secondary tissue consisting of alternating bands of lignified fibers and vessels, and nonlignified parenchyma and phloem (Maheshwari; Balfour; Studholme & Philipson). Most studies of anomalous secondary growth in the family have dealt mainly with the initiation of the primary thickening meristem and its derivatives in mature stems, but recent interest has turned to its initiation in the major organs of the seedlings. Mikesell & Popham found that in seedlings of *Mirabilis Jalapa* the primary thickening meristem first appears in the base of the stem. Subsequent development is acropetal in the stem and basipetal into the hypocotyl and root, where further differentiation is also acropetal. This sequence differs slightly in seedlings of *Bougainvillea spectabilis*, where the primary thickening meristem first appears at the base of the primary root and later at the base of the hypocotyl. Secondary vascular bundles (desmogen strands) arising from meristematic activity in stems of *B. spectabilis* exhibit limited cambial activity, producing tertiary xylem and phloem cells (Stevenson & Popham). Length of photoperiod has been shown to affect cell size and time of lignification in conjunctive tissue of hypocotyls and root bases of *Mirabilis Jalapa* seedlings (Mikesell & Popham).

Stomatal structure and ontogeny vary among the genera, with both anomocytic (ranunculaceous) and paracytic (rubiaceous) types recorded (Metcalf & Chalk). Inamdar reports a perigenous ontogenetic pattern for both types in three genera of the family.

In the fledgling field of ultrastructural systematics Behnke (1969, 1972) has described "P-type" plastids, i.e., leucoplasts that elaborate primarily proteinaceous inclusions, rather than starch granules as in "S-type" plastids, in the sieve tubes of *Mirabilis longiflora* L., and *Pisonia Brunoniana* Endl. Calcium oxalate raphide crystals are particularly abundant throughout plants of *Boerhavia*, and are also abundant in *Bougainvillea*, *Mirabilis*, *Okenia*, and *Pisonia* (Heimerl, 1890).

The family is of no economic significance apart from a few widely cultivated ornamental species of *Abronia* (Sand Verbena), *Mirabilis* (Four-o'clock), both annuals, and *Bougainvillea*, a woody vine. Less often plants of the herbaceous *Boerhavia* or woody *Pisonia* may be found in cultivation.

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KEY TO THE GENERA OF NYCTAGINACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *Annual or perennial herbs or shrubs, trees, or woody vines with mostly opposite (to alternate) simple, entire to sinuate, exstipulate leaves; inflorescences terminal or lateral, basically cymose, bracteate to involucrate, the involucres containing 1 to several flowers; flowers perfect or imperfect, small and inconspicuous to large and showy, regular, hypogynous; sepals 5, united, fleshy and inconspicuous to membranaceous and corolla-like, constricted above the ovary, the limb ephemeral; corolla lacking; stamens 1 to many, or few, reduced, and sterile, unequal, free or basally united, the anthers didymous; carpel solitary, the ovary unilocular; ovule 1, basal. Fruit accessory, the accrescent calyx base berry-like to hard and leathery, inclosing the fruit (an achene or utricle).*

A. Plants herbaceous, or woody only at the base; flowers perfect; stigma capitate; embryo curved.
  B. Flowers involucrate, involucres solitary in leaf axils or in terminal or lateral loose to congested cymes; involucres 1 to several flowered.
    C. Involucral bracts 5, united, calyx-like, campanulate to rotate and veiny in fruit; flowers 1 or 2–6 per involucre; stamens 3–5. . . . . 1. *Mirabilis.*
    C. Involucral bracts 3 or 4, small, free; flowers solitary, axillary; perianth densely pubescent without; stamens 9–18; pedicels elongating after flowering, the fruit hypogeous. . . . . 2. *Okenia.*
  B. Flowers exinvolucrate, numerous, small (less than 1 cm.); inflorescence a diffuse lateral or terminal cyme, the ultimate flower clusters usually subumbellate; stamens 1–3(–5). 3. *Boerhavia.*
A. Plants woody, sometimes armed; flowers usually imperfect; stigma penicillate; embryo straight. . . . . 4. *Pisonia.*

Tribe NYCTAGINEAE [Mirabileae Meissner]

Subtribe **Nyctagininae** [Boerhaviinae Bentham & Hooker]

1. **Mirabilis** Linnaeus, Sp. Pl. 1: 177. 1753; Gen. Pl. ed. 5. 82. 1754.

Annual or perennial herbs with one to numerous stems from a tuberous root or woody rootstock; the stems stout or slender, slightly 4-angled, simple or dichotomously branched, erect or decumbent, as much as 1–2 m. high, densely pubescent, pubescent in lines, or glabrous, sometimes viscid

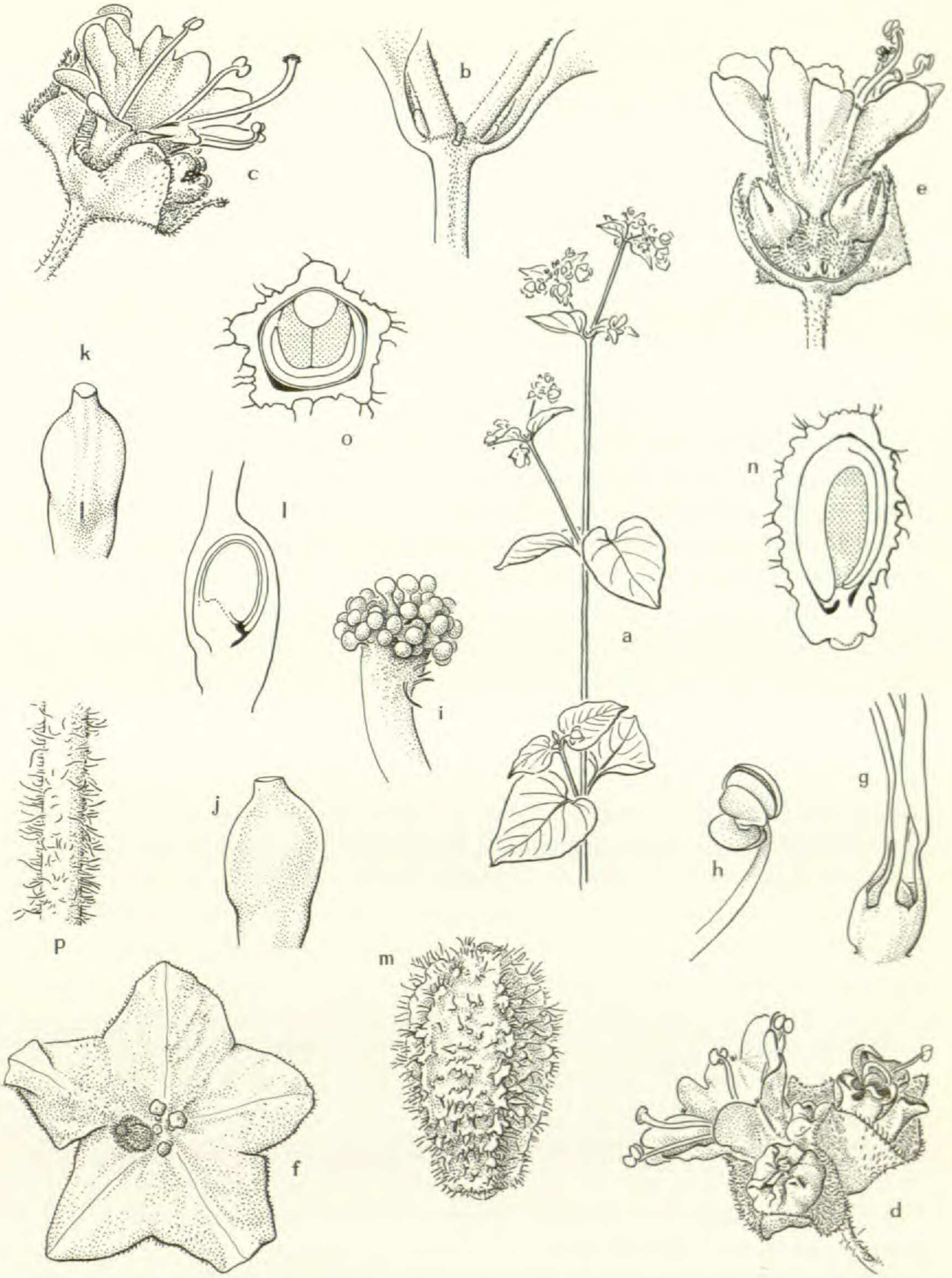

FIGURE 1. **Mirabilis.** a–o, *M. nyctaginea*: a, flowering branch, × 1/4; b, leaves at base of inflorescence with aborted terminal flower, × 2; c, d, two views of cymule of flowers with involucre, × 3; e, same, lateral view, portion of involucre removed to show flower and two buds, × 3; f, involucre from above, showing developing fruit and pedicels of three unpollinated flowers, × 2; g, base of androecium showing connation of staminal filaments around ovary, × 12; h, anther after dehiscence, × 12; i, stigma, × 25; j, k, two views of ovary, × 25; l, ovary in diagrammatic vertical section, showing basal ovule, × 25; m, mature accrescent calyx base inclosing fruit, × 10; n, same in vertical section showing fruit with embryo surrounding perisperm (stippled), ovary wall and seed coat too thin to be shown except at base, × 10; o, same in cross section, the embryo cut through cotyledons and hypocotyl, perisperm stippled, × 10. p, *M. hirsuta*: portion of stem, hairy, in contrast with stem of *M. nyctaginea*, × 2.

or glaucous, nodes slightly swollen; leaves opposite, exstipulate, petioled or sessile, entire; inflorescence an axillary or terminal, loose or congested thyrsiform or paniculate cyme of involucrate flowers, or involucres solitary in the axils; involucres one to few flowered, calyx-like, 5-lobed, the lobes equal or unequal, erect, imbricate in bud, green (the margins sometimes tinged purple) glabrous or pubescent, ± campanulate, often accrescent, becoming rotate and conspicuously veiny in fruit; flowers perfect, calyx tubular, corolla-like, the tube mostly very short, in a few species long to very long (3–17 cm.), constricted above the ovary, the limb campanulate to funnel-form or rotate (or not conspicuously expanded), 5-lobed, the lobes retuse or emarginate, induplicate-valvate or -plicate, the perianth ephemeral, falling after anthesis but the base persistent about the ovary and thickening in fruit; stamens 3–5, hypogynous, free or basally connate, filaments capillary, unequal, anthers didymous, exserted, dehiscing by slits; pollen polyporate; ovary superior, sessile, of one carpel; style filiform, longer or shorter than the stamens, stigma capitate, papillose; ovule solitary, anacampylotropous, integuments two; fruit accessory, the persistent calyx tube thickened, hard or leathery, 5-angled or -ribbed, the angles and surfaces smooth, rugose, or verrucose, pubescent or glabrous, the ovary wall membranaceous; embryo ± folded, cotyledons foliaceous, unequal (the inner smaller), curved around an abundant perisperm, radicle about as long as the cotyledons. (Including *Allionia* Loefl. [not *Allionia* L., nom. cons.]), *Oxybaphus* L'Hér., *Calymenia* Pers., *Jalapa* Miller, *Nyctago* Juss., *Trimista* Raf., *Admirabilis* Nieuwl.) TYPE SPECIES: *M. Jalapa* L. (From Latin, wonderful, presumably in reference to the large colorful flowers of *M. Jalapa.*) — Four-o'clock, marvel of Peru, umbrella-wort.

A New World genus of perhaps 45(–60) species, disposed most recently in six sections (Heimerl, 1934). The genus is best developed in southwestern North America but ranges from southern Canada and New England south to southern South America, with one species in Asia. As many as thirty-two species (under several generic synonyms) have been reported from the southwestern United States (Standley, 1918), but only five occur in our area.

Section MIRABILIS (sect. *Eumirabilis* Hook. f. in Heimerl, 1934) is characterized by one-flowered, more or less campanulate involucres that change little in fruit. Each flower has a conspicuous corolla-like, salverform, or funnel-shaped (to almost cylindric) calyx, five stamens, and a nonmucilaginous, glabrous or hairy, angled or ribbed, smooth or warty accessory fruit. The section is represented in our area only by *Mirabilis Jalapa,* four-o'clock or marvel of Peru, $2n = 54, 58$, a popular garden annual (or perennial in warmer regions). The erect, much-branched, tuberous-rooted plants of this species reach a meter in height, bear mostly ovate-deltoid to broadly ovate, glabrous, petiolate leaves with subcordate to rounded bases, and flowers with a showy salverform calyx tube 3–6 cm. long, which varies in color from purplish to red, yellow, white, or variegated. The species escapes from cultivation and is naturalized in waste places in some areas of the Southeast.

The four remaining species of our area were assigned by Heimerl (1934) to sect. EUOXYBAPHUS Heimerl, which contrasts with section MIRABILIS in having 2–6-flowered, campanulate involucres that become enlarged, veiny, and more or less rotate at maturity; a shorter campanulate to funnelform (or rotate) calyx limb that lacks a long tube and is deeply constricted above the ovary; 3–5 stamens; and fruit with a strongly 5-ribbed, usually hairy calyx base that becomes gelatinous when wet. *Mirabilis nyctaginea* (Michx.) MacM. (*Allionia nyctaginea* Michx., *Oxybaphus nyctagineus* (Michx.) Sweet), wild four-o'clock or heart-leaved umbrellawort, $2n = 58$, forms stout, erect, much-branched glabrous (or pubescent in lines above) plants bearing definitely petioled, usually deltoid-ovate leaf blades with rounded to cordate bases, pedunculate, congested-cymose inflorescences, basally short-pilose or puberulent involucres, magenta to pale-pink (or white) calyx tubes about 10 mm. long, and a fruit with a densely short-pilose obovoid calyx base with more or less rugose angles. It prefers rich soil in dry open ground in prairies and waste places, ranging in our area from Alabama to Louisiana and Arkansas, westward to Texas and Mexico, northward east of the Rocky Mountains to Tennessee, Wisconsin, Manitoba, and Montana. To the east and west it is reported as a rare adventive weed of waste places, especially along railroad beds and roadsides. *Mirabilis albida* (Walter) Heimerl (*Allionia albida* Walter, *Oxybaphus albidus* (Walter) Sweet) is a variable species having more or less glabrous stems bearing inconspicuous hairs in two lines along the internodes; sessile or nearly sessile leaves with usually lanceolate blades about 4–12 times longer than broad that vary in shape from linear-lanceolate to narrowly elliptic or oblong; a white or pale-pink perianth about 8–10 mm. long; and fruiting calyx bases with tuberculate angles. The species ranges from Georgia to Texas, northward to South Carolina, Tennessee, Iowa, and Kansas. It is usually found in open ground in prairies and meadows, the edges of bluffs, and limestone glades, as well as in waste places.

The stems of *Mirabilis hirsuta* (Pursh) MacM. (*Allionia hirsuta* Pursh, *Oxybaphus hirsutus* (Pursh) Sweet) are conspicuously and often densely pubescent or viscid pubescent. The pubescent leaves are sessile or borne on short, stout petioles, with broadly to narrowly ovate, cuneate, or linear-lanceolate blades, truncate to rounded or attenuate bases, and gradually narrowed, obtuse apices. The mostly three-flowered, viscid-pilose involucres may be solitary and axillary on younger plants, or grouped in diffuse, long-pedunculate thyrsiform or paniculate cymes on mature plants. The white to pink calyx tubes are 8–10 mm. long, and have 3–5 exserted stamens. In fruit, the accrescent calyx bases have more or less smooth angles and warty surfaces. A species of the Great Plains, *M. hirsuta* occurs in dry, open soil of prairies, sandhills, and gravelly areas and is probably adventive in our area from its native range, which extends from Texas, Oklahoma, and western Missouri, northward to Wisconsin and

Saskatchewan, and westward to the Rockies. *Mirabilis linearis* (Pursh) Heimerl (*Allionia linearis* Pursh, *Oxybaphus linearis* (Pursh) Robinson), $2n = 52$, is distinguished by its thick, linear leaves 5–15 cm. long and usually less than 5 mm. broad. The stems are usually glabrous (sometimes puberulent in lines) and often slightly woody below, developing from a woody rootstock. The pale-pink to purplish-red perianth is about 10 mm. long, and the perianth base in fruit is smooth angled. This species is apparently a rare adventive in our area from its range in western Missouri, Oklahoma, Arizona, and Mexico, northward to Minnesota and Montana (Steyermark, 1963).

Taxonomic opinion has varied as to the number of genera represented in the *Mirabilis* group. Gray (1859) separated *Mirabilis* (incl. *Quamoclidion* Choisy) and *Oxybaphus* (including the four indigenous species of our area) on characters of the involucre, stamen number, and fruit, while Heimerl (1889) recognized only *Mirabilis* (incl. *Oxybaphus*, *Quamoclidion*). Many species now included in *Mirabilis* have synonyms in *Allionia* Loefl., *Allioniella* Rydb., *Hesperonia* Standley, *Oxybaphus* L'Hér., and *Quamoclidion* Choisy. All of these genera were recognized by Rydberg (1902) and by Standley (1909, 1911, 1918) in his earlier papers. However, Standley (1931), the principal American student of the family, finally concluded that "If only the species of North America are considered, such genera as *Oxybaphus*, *Quamoclidion*, and *Hesperonia* seem to be differentiated by good and constant characters; but as so often happens, when extra limital species are taken into account, the characters supposed to separate the groups break down. It seems necessary, therefore, to follow Heimerl in considering all the plants of the group as repsenting a single genus." In his last revision of the genus Heimerl (1934), the leading European student of the family, recognized about 60 species arranged in six sections. Subgenera were recognized in *Mirabilis* (excl. *Oxybaphus*) by Gray (1859), Jepson (1909), and Macbride (1917, 1918). Shinners (1951) considered the species of *Oxybaphus* to be quite distinct, but satisfactory as a subgenus of *Mirabilis*. Most authors now recognize only *Mirabilis* (e.g., Reed, 1969), but *Oxybaphus* has been maintained as distinct from *Mirabilis* on a traditional basis in some recent floristic works, with the acknowledgment that the two might better be united (Gleason, 1952; Gleason & Cronquist, 1963).

Shinners noted that extreme seasonal, genetic, and environmental polymorphism exists in most of the species. He suspected hybridization in the genus, particularly in *Mirabilis albida*, which shows variation suggesting the influence of *M. linearis* and *M. gigantea* (Standley) Shinners, and possibly other species. A modern systematic study and revision of the genus is needed.

Chromosome counts recorded for six species of the genus show $2n =$ 52, 54, or 58 (Bolkhovskikh, Bowden, Löve & Löve).

Related genera include *Allionia* L. (nom. cons., *A. incarnata*, $2n =$ ca. 58; incl. *Wedelia* Loefl., and *Wedeliella* Cockerell), which can be distinguished by its usually three-flowered, three-parted involucres of fused bracts, and compressed fruits bearing two rows of stipitate glands on the dorsal surface of the calyx base, and the monotypic *Hermidium* S. Watson (*H. alipes* S. Watson), in which the flowers are aggregated in headlike clusters and the pedicel of each flower is adnate to the midrib of a subtending foliaceous bract. Barneby (1942) suggested that *Hermidium alipes* is morphologically little more than a primitive relative of "subgenus Quamoclidion" and should be united with *Mirabilis*.

The best known species is *Mirabilis Jalapa* ($2n = 58$). Because of its easy cultivation it has been the subject of numerous investigations in many fields. It figured significantly in early genetic investigations on the inheritance of flower color (see Heimerl, 1934, p. 109, for citations of early literature; Kiernan & White, 1926; Showalter, 1934b). Although largely attributable to Mendelian inheritance patterns, non-Mendelian variation in flower color and plant habit due to somatic or gametic mutation has also been reported (Showalter, 1934a, b; Nakajima, Melcher). Clute reported a case of amphichromy, with both red and white flowers on the same plant, and even in the same cluster.

Hybrids between cultivated plants of *Mirabilis Jalapa* and *M. longiflora*, $2n = 54, 58$, have been known since the mid-eighteenth century, and have also been synthesized and studied extensively with regard to the cytological aspects of hybrid sterility (Tischler, Prakken), and to hybrid variation and the inheritance of parental characteristics (Prakken, Bazavluk, Kruszewska). Jost found that the cross *M. Jalapa* × *M. longiflora* works, but that the reciprocal cross never succeeds because the pollen tube of the relatively short-styled *M. Jalapa* stops growing before it has traversed the length of the much longer style of *M. longiflora*, thus preventing fertilization.

In the developing seedling of *Mirabilis Jalapa* a transition from monopodial to falsely dichotomous sympodial branching occurs between the level of the cotyledons and the fifth node. This change is brought about by the inhibition of the terminal apex and the accelerated development of the two lateral axillary buds at each node. It is accompanied by a change in the organization of the apical meristem that persists until the appearance of the first (terminal) flower (Champagnat & Laurent). Other morphological and anatomical studies dealing with *M. Jalapa* include those of Beal & Whiting; Champagnat, Champagnat, & Laurent; Lloyd; Mirskaja; Morot; Regnault; Vardar; and Wibaut.

Clements described in detail the histogenesis of the root-stem transition zone, lateral roots, and vegetative apex in *Mirabilis hirsuta* and *M. nyctaginea*. The ontogeny and course of the complex primary vascular system of the internodes, nodes, petioles and lateral branches of *M. Jalapa* is described by Inouye. Secondary tissues are derived from a primary thickening meristem that in *M. Jalapa* is extrafascicular in origin, developing acropetally in the stem and downward through the hypocotyl into the root, where further growth is also acropetal (Maheshwari; Mikesell & Popham).

Floral ontogeny is acropetal in sequence, the carpel arises on one side of and gradually incloses an apparently terminal nucellus. The carpel margins are fused in *Mirabilis Jalapa*, but are free for a short distance in *M. nyctaginea* (as *Oxybaphus Cervantesii*), forming a small pore (Payer). Heimerl (1887) described and illustrated in detail the anatomy and development of the flowers and fruits of *M. Jalapa, M. longiflora,* and *M. nyctaginea.* According to Joshi & Rao, the perianth of *Mirabilis Jalapa* is supplied by ten traces arising as two pentamerous cycles from the pedicellar stele, while a series of five stamen-traces originates above and opposite the upper set of perianth traces. A single (dorsal) bundle supplies the carpel, providing one trace to the basal ovule. Both the accrescent calyx base and the basal "coalesced" portion of the androecium which bears nectariferous tissue on its inner surface are interpreted by Buxbaum as being outgrowths of the floral axis rather than modifications of the perianth and androecium. The anatomy of the style and stigma of *M. Jalapa* are described by Guéguen.

The earlier embryological literature on the genus was reviewed by Rocén, who described the details of development and structure of the stamens, carpels, ovules before and after fertilization, and that of the endosperm for eight species of *Mirabilis* and *Oxybaphus* (including *M. Jalapa* and *M. nyctaginea*). Development of the female gametophyte is of the Polygonum type, and two gametophytes are sometimes formed. Each locule of the tetrasporangiate anther of *M. nyctaginea* contains 8–24 large pollen grains that are 3-celled when shed (Cooper). During embryo development (Asterad type) almost all the free-nuclear endosperm is absorbed by the embryo. Only a small portion of the endosperm becomes cellular; this persists as a cap over the tip of the radicle. The pollen tube is stated to persist throughout seed development, functioning as a haustorium in the transfer of nutrient materials from secretory cells of the funiculus to the developing embryo (Cooper; Hedeman; Schnarf; Woodcock). The stalk of the mature ovule is densely packed with white raphide crystals (Pobeguin, Cooper).

One of the most interesting morphological features of the genus is the progressive reduction in the number of flowers (as many as 12) included within the involucre, culminating in the one-flowered inflorescences evident in sect. MIRABILIS, in which the involucre imitates a calyx and the calyx a brightly colored corolla. The flowers of *Mirabilis* are ephemeral, opening in the late afternoon or evening and closing by early to mid-morning. The time of anthesis varies among the species (Kerner, Cruden), and poor weather conditions may delay opening and closing of flowers. The time of anthesis may also be genetically controlled, with continuous variation demonstrated among F_1 hybrid progeny resulting from crosses between *M. Jalapa* and *M. longiflora* (Kruszewska). The mechanism controlling anthesis is not known, but Meeuse concludes that the daily flowering time of *M. Jalapa* may be determined by the time of sunset on the preceding day.

Both self-compatible (*M. Jalapa, M. longiflora, M. nyctaginea, M. violacea*) and self-incompatible (*M. Froebelii, M. Greenei, M. multiflora*) breeding systems are reported in the genus (Kerner; Baker, 1961, 1964; Cruden, 1973). In *M. nyctaginea* pollination is by bees in both afternoon and morning and by small noctuid moths at night. Chasmogamous flowers are produced in early summer, cleistogamous ones in later summer. Chasmogamous flowers can be self pollinated as the flower closes, the coiling of the style and then the stamens bringing the stigma in contact with the pollen. (Cruden, 1973). Both insect pollination and self pollination are recorded for *M. Jalapa*. As the flower closes the coiling of the style carries the stigma through the stamens at least once, sometimes twice (Cruden, 1973; Heimerl, 1888).

Hawkmoths pollinate the white, night-blooming flowers of *M. longiflora* and *M. multiflora*, while hawkmoths and hummingbirds are the principal pollinators for *M. Froebelii*, along with bees and butterflies (Kerner; Baker, 1961; Cruden, 1970). The "apparent" tristyly observed in *M. Froebelii* by Baker (1964) is suggested by Bateman to be an early stage in speciation by divergent adaptation to different pollinators. Cruden (1970) suggests that selection for a single class of pollinators (hawkmoths) has occurred in *M. multiflora*.

Species of *Mirabilis* have long been cultivated as garden annuals or for use in folk medicine. *Mirabilis Jalapa* was introduced into European horticulture, supposedly from Peru, in 1596 (Curtis, 1797; Showalter, 1934b). However, a plant reputed to be *M. Jalapa* is illustrated in the Badianus Manuscript (ca. 1552; cf. Emmart), and Standley (1931) suggested that the species may have originated in Mexico, since its nearest relatives are indigenous there, while none occur in Peru. The specific epithet derives from the very early but erroneous belief that this species was the source of the medicinal resin "Jalap," the actual source of which is *Exogonium Purga* (Hayne) Lindley, of the Convolvulaceae (Hill, 1952). *Mirabilis nyctaginea* was also early cultivated in European botanical gardens, and some species, e.g., *Oxybaphus floribundus* Choisy, were described from such plants (Shinners). About ten species or hybrids of the genus are now cultivated as ornamentals (Bailey & Bailey; Chittenden). In areas where the plants are not hardy the fleshy roots can be lifted in the fall and stored over the winter like *Dahlia* roots.

Apart from its horticultural value the genus is of no economic importance. The roots of *Mirabilis Jalapa* are mildly purgative and are also used in folk medicine for dropsy. The leaves are bruised or ground for use in poultices for boils, abscesses, and scabies. When steeped in water the flowers provide a crimson dye used in China for tinting cakes and also jellies prepared from seaweed. A cosmetic powder is made in Japan from the powdered seeds (Stemmerik, Uphof).

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2. **Okenia** Schlechtendal & Chamisso, Linnaea **5**: 92, 93. 1830.

Densely and finely glandular-pubescent annual herbs, with diffuse prostrate branches 2–7 feet long radiating from a short ligneous caudex on a long narrow taproot, forming mats. Leaves opposite, markedly unequal, the large and small alternating in position on the stem, the smaller often not as long as the petiole of the larger; petioles long, stout, exstipulate; blades ovate-deltoid, ovate or elliptic-ovate, the base rounded, truncate, or subcordate, sometimes inequilateral, the apex acute to rounded, the

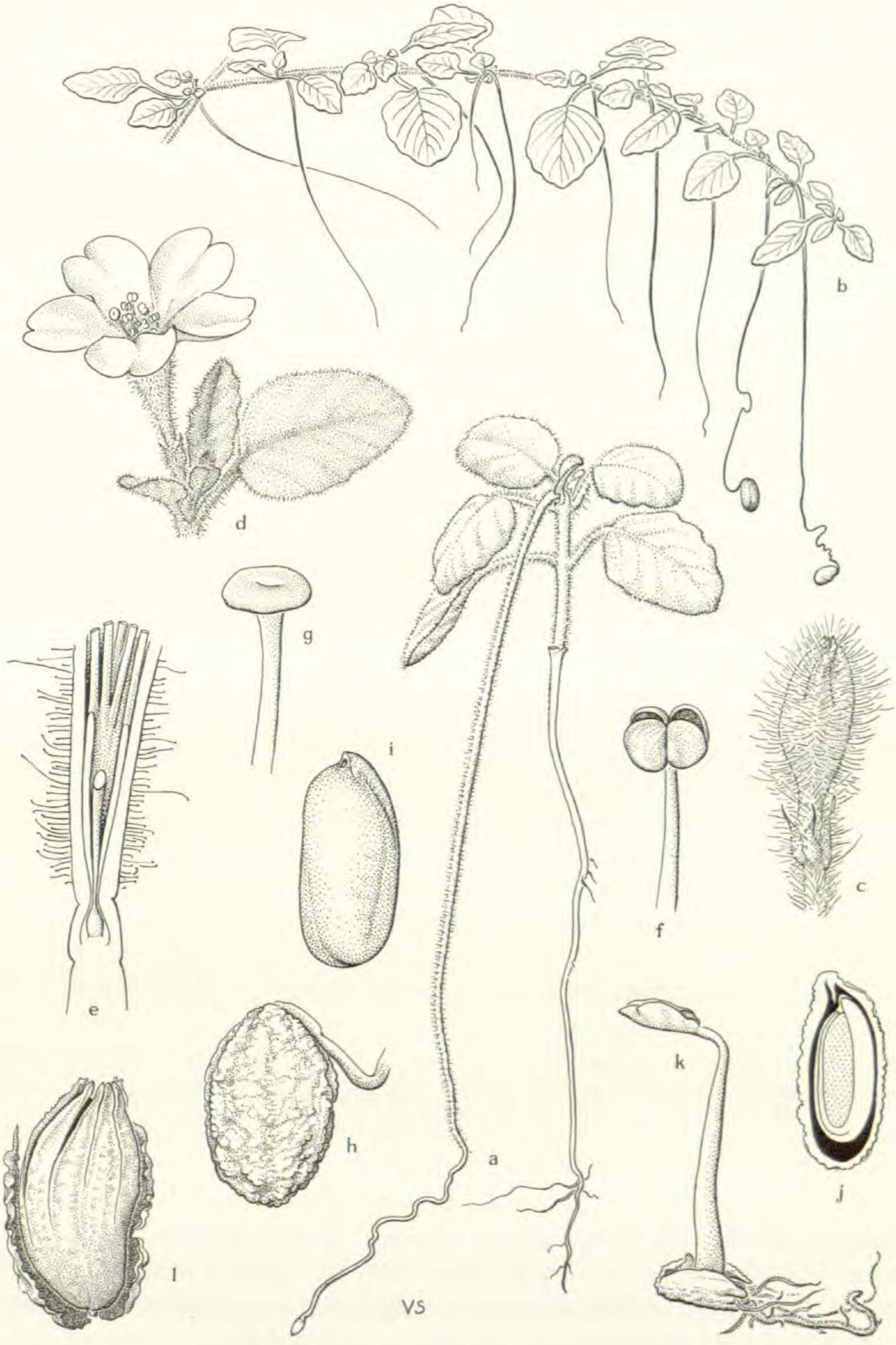

FIGURE 2. **Okenia.** a–l, *O. hypogaea*: a, seedling (in July) bearing developing fruit from first flower, the peduncle greatly elongated, × 3/4; b, branch from prostrate fruiting plant (in October) with two mature fruits and withered peduncles of earlier fruits, × 1/3; c, bud with bractlets, × 3; d, open flower, × 1 1/2; e, lower part of flower in partial section to show connation of staminal filaments — note ovary free from stamens and calyx base, × 12; f, anther, × 12; g, stigma, × 12; h, nearly mature accessory fruit, × 2; i, mature fruit removed from accrescent calyx base, × 3; j, mature accessory fruit in vertical section to show embryo surrounding perisperm (stippled), × 2; k, seedling with remains of calyx base, × 1; l, remains of calyx base after germination of seed, × 3.

margin entire to shallowly sinuate; both surfaces densely viscid-villous, the epidermis marked by the small brown dots of the trichome bases. Flowering stems axillary, ascending at anthesis, later deflected, pushing underground. Flowers incomplete, perfect, cleistogamous (?); terminal, solitary at each node, on long, often naked peduncles axillary to the small leaf of each pair, subtended by an involucre of 3–4 small, narrow, subulate bracts and a short pedicel. Sepals 5, united in a short, slender, funnelform tube, densely pubescent without, constricted above the ovary, 5-lobed, the lobes notched, brilliant magenta [dark blue to violet or white]; earlier flowers 25–30 mm. in diameter, later flowers much smaller; aestivation induplicate-plicate. Stamens 9–18; filaments filiform, unequal, united below into a short tube, magenta above to white below; anthers didymous, the lobes subglobose, attached to each other and the filament at the middle, dehiscing laterally by simple longitudinal slits. Style filiform, long; stigma large, capitate-peltate. Ovary small; ovule campylotropous (?). Fruit hypogeous, the thin-walled pericarp enclosed in the ± oblong thickened corky base of the calyx tube that is longitudinally ribbed, transversely plicate between the ribs, dark brown to whitish. Embryo peripheral, conduplicate; cotyledons large, obovate, unequal, enclosing the starchy perisperm; radicle about as long as the cotyledons, ascending. TYPE SPECIES: *O. hypogaea* Schlechtendal & Cham. (Named after the German naturalist Lorenz Oken, 1779–1851). — Dune-groundnut.

A very small and little-known genus, probably of two species, best known in our area as a maritime dune-plant on the Keys of southeastern Florida, where it is represented by the type species. The genus is also distributed in Mexico on both the eastern and western coasts and in the interior.

Standley (1911) described two new species (*O. grandiflora* and *O. rosei*) from specimens collected in Jalisco, Mexico, but later (1918) reduced them to synonymy under *O. hypogaea*. More recently, Wilson (1958) described *O. parviflora* P. G. Wilson from inland Mexico (Michoacán, Guerrero), a plant that is said to differ from *O. hypogaea* in its much smaller flowers and fewer (ca. 5) stamens.

The genus is notable for its subterranean fruits, which mature at depths of 10–30 cm. below the surface and germinate in place to give rise to new plants. After the ephemeral corolline calyx tube has fallen the peduncle becomes deflected and, through rapid elongation, pushes the developing fruit inclosed in the calyx base beneath the surface of the sand. A conical cap of cells, much like a thick root-cap, develops over the tip of the calyx base, protecting the ovary from abrasion as it is pushed beneath the sand (Karsten). Heimerl (1911) published brief observations on the morphology and anatomy of the fruit, seed, embryo, and seedling, but the vegetative anatomy, embryology, and chromosome number of the genus are apparently unknown. This interesting genus requires further study, particularly with regard to its floral biology and its taxonomy in Mexico.

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3. **Boerhavia** Linnaeus, Sp. Pl. **1**: 3. 1753; Gen. Pl. ed. 5. 4. 1754.

Annual or perennial, glabrous, pubescent, or glandular herbs, often much branched from a narrow taproot or thickened woody rootstock; stems slender, diffuse, erect, ascending or decumbent, becoming ± woody below with age, the nodes swollen. Leaves simple, opposite, exstipulate, petiolate, those of a pair unequal, the large leaves alternating on the stem; blades gradually reduced upwards on the stem, slightly thickened, sometimes inequilateral, pinnipalmately veined, sometimes minutely dark dotted below, often tinged purplish, in outline broadly to narrowly deltoid, ovate-deltoid, or ovate to elliptic-oblong or linear-lanceolate above; margins entire; apex rounded or obtuse to acute, often mucronate; base subcordate or truncate to rounded or in the upper leaves acutely tapering. Lateral branches alternating on the stem, developing from the axil of the smaller leaf, accompanied by a short, deciduous, extra-axillary branch. Inflorescence lateral or terminal, cymose, paniculiform or thyrsiform, bracteate or bracteolate, ± diffuse, the ultimate flower clusters often subumbellate. Flowers small, perfect, sessile or on short- to long-jointed, accrescent pedicels, subtended by 1–3 small bracteoles; perianth tubular below, ± thick, 4–5[–10]-ribbed, glabrous or glandular-pubescent along the ribs, constricted near the middle around the top of the gynoecium, the limb campanulate, corolla-like, ± 5-lobed, aestivation plicate, white or pink to lavender or purple, limb deciduous. Stamens 1–3[–5], hypogynous, filaments slender, free or united basally in a shallow tube around the gynophore, anthers exserted, 4-sporangiate, 2-loculate at anthesis, didymous, dehiscing by simple slits; pollen forate, binucleate (sometimes trinucleate) when shed. Ovary shortly stipitate; style filiform; stigma capitate-peltate, slightly exserted; ovule anacampylotropous, with a single integument. Accrescent calyx base fleshy, clavate or obovate to narrowly obpyramidal, closed at the apex, 4 or 5[–10] ribbed, glabrous or sparsely

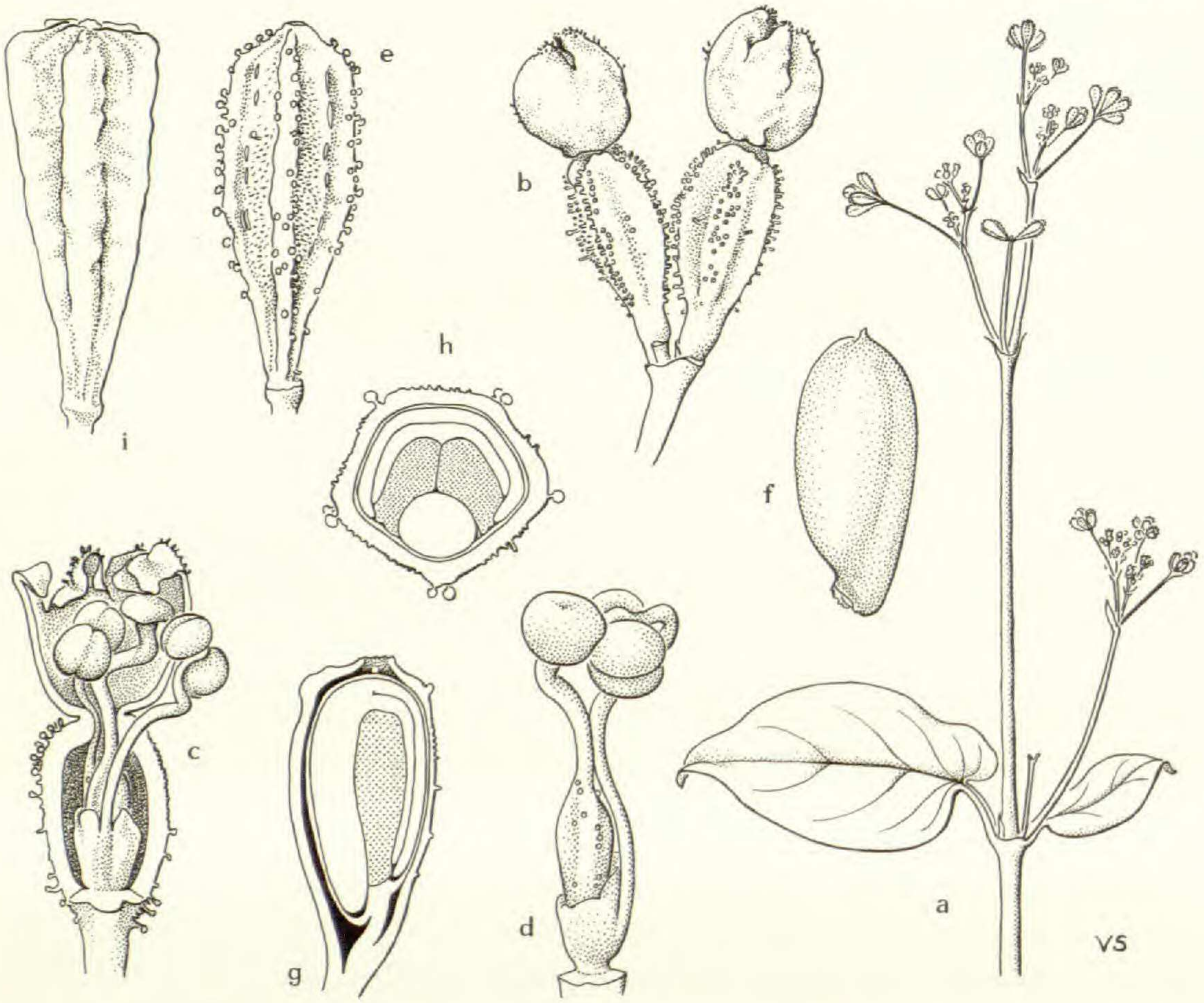

FIGURE 3. **Boerhavia.** a–h, *B. diffusa*: a, tip of flowering stem, × 3/4; b, two flowers, × 12; c, flower in vertical section to show perianth tube surrounding androecium and gynoecium, × 15; d, gynoecium and one of four stamens, three removed, × 25; e, accrescent calyx base inclosing fruit, × 12; f, fruit, × 12; g, calyx base and fruit in vertical section, the embryo white, the perisperm stippled — note that calyx is not adnate to fruit, × 12; h, same, in cross section, cotyledons of embryo above, hypocotyl below, × 15. i, *B. erecta*: mature accrescent calyx base inclosing fruit, × 12.

glandular pubescent, the grooves sometimes transversely wrinkled or longitudinally streaked with white raphides, falling with the inclosed fruit at maturity. Fruit a utricle, carpel wall membranaceous; embryo longitudinally folded at the hypocotyl, radicle straight, cotyledons unequal, curved inward around a columnar, mealy perisperm. LECTOTYPE SPECIES: *B. erecta* L.; see Standley, Contrib. U. S. Natl. Herb. 12: 375. 1909. (Named in honor of Herman Boerhaave, 1668–1738, Dutch naturalist and Professor in Leiden.) — Spiderlings, Wine-flower.

A weedy genus of perhaps 3–30 species distributed in the tropical and subtropical regions of the world, but best developed in southwestern North America. Up to fifteen species have been recognized in the southwestern United States (Tidestrom & Kittell, 1941). Two species occur as weeds of waste places in our area.

The morphologically variable pantropic weed *Boerhavia diffusa* L. (incl.

B. caribaea Jacq., *B. coccinea* Miller, *B. decumbens* Vahl, *B. hirsuta* Willd., *B. paniculata* Rich., *B. viscosa* Lag. & Rodr.), wine-flower, of sect. CLAVATAE of Heimerl (1934), is a prostrate to ascending, often viscid-pubescent weed of cultivated ground, pinelands, and waste places, with reddish-green to red or purplish [rarely white] flowers. Its narrowly obovoid 4- or 5-ribbed calyx bases have more or less rounded apices and bear short-stalked capitate glandular hairs along the ribs. It is widely distributed in Florida, but apparently infrequent in the Gulf States, and ranges westward to Texas and southern California, and southward to the West Indies, Mexico, Central America, and South America. *Boerhavia erecta* L., spiderling, of sect. PYRAMIDATA of Heimerl (1934), is an erect or ascending, essentially glabrous annual up to 1 m. tall, with leaves characteristically minutely and darkly spotted below, white or cream to pink or pale lavendar flowers, and narrowly obpyramidal, truncate, and glabrous accrescent calyx bases. It is also a pantropical weed, distributed in the southern United States from Florida to Texas and Arizona, northward along the Coastal Plain to North Carolina, in the Piedmont to South Carolina, and in the Mississippi embayment to Missouri, Arkansas, and Oklahoma. It extends southward in the Antilles, Mexico, and Central America to the tropics of South America.

The systematics of the genus is chaotic and badly in need of critical study. Heimerl (1889) divided twenty species of *Boerhavia* among five sections, but later (1897) reduced the sections to four. Three of these were subsequently segregated by Standley (1909, 1911), as genera of questionable validity. *Anulocaulis* Standley (1909) (sect. *Solenanthe* Heimerl, 1889) was considered distinct from *Boerhavia* in its large, thick leaves, distinctly tubular perianth, 10-ribbed turbinate or biturbinate fruits, and sticky-banded internodes. The plants appear to be obligate gypsophiles (Waterfall, 1945). About five species have been described (Waterfall, 1945; Johnston, 1944). *Commicarpus* Standley (sect. *Adenophorae* Heimerl) was set apart on the basis of a climbing or reclining habit, short funnelform perianth, and weakly 10-ribbed clavate fruits bearing numerous large mucilaginous glands. About sixteen species have been recognized, ranging from the southwestern United States, the Antilles, and Mexico, southward to northern South America, as well as in Africa, the Middle East, and Asia (Heimerl, 1934; Balle, 1951). *Cyphomeris* Standley (1911) (sect. *Senckenbergia* of Heimerl; incl. *Lindenia* Mart. & Gal., *Tinantia* Mart. & Gal., *Senkenbergia* Schauer), has been distinguished by its asymmetrical, clavate eglandular calyx bases and racemose inflorescences. Two species are known from Texas, New Mexico, and Mexico.

Heimerl (1934) accepted these segregates and revised the remaining species (sects. PTEROCARPON and MICRANTHAE, 1889), establishing four sections, but various authors of regional floras have rejected the segregates in whole (Tidestrom & Kittell, 1941) or in part, and the number of species recognized in *Boerhavia* varies accordingly. Standley later (1931) reduced *Commicarpus* to synonymy under *Boerhavia*, a course also followed by Stemmerik (1964 a,b), but some other workers maintain the genus. Several recent authors (Balle, 1951; Stemmerik, 1964; Woodson, 1961) have concluded that only two (or three if *Commicarpus* is included) variable, pantropic species constitute the genus *Boerhavia* proper. Woodson found "no tangible differences between *B. caribaea* and *B. coccinea* of the New World and *B. diffusa* of the Old World," and recognized only *B. diffusa* and *B. erecta*. This view is adopted here.

The generic name frequently appears in the literature with the spelling *Boerhaavia*, but Linnaeus latinized Boerhaave's name to "Boerhavius," and deliberately adopted the spelling *Boerhavia*, which should be used (Sprague, 1928). Although *B. erecta* L. is the accepted lectotype (Standley 1909), *B. repens* L. (Standley, 1918; Abrams, 1944), and *B. diffusa* L. (Hitchcock, 1930) have also been cited as "types."

Widely differing chromosome numbers are reported for the genus, including $2n = 26$ and 116 for *Boerhavia diffusa* L., $2n = 42$ for *B. repanda* Willd. (*B. chinensis* of Stemmerik, 1964), and $2n = 40$ for *Commicarpus tuberosus* (Lam.) Standley (*B. tuberosus* Lam.). I know of no counts from species of the southern United States.

Woodson (1961) suggests that hybridization probably occurs between *B. diffusa* and *B. erecta* in areas where they grow together, but that it is not sufficient to blur the species lines.

A diffuse vascular system and anomalous secondary growth characterize the stems of *Boerhavia diffusa* and *B. repanda* (Maheshwari, 1929, 1930; Bhargava, 1932) and give rise to a complex nodal anatomy, with 1–3 (*B. diffusa*) or 5 (*B. repanda*) leaf traces supplying the petiole. The leaf traces are derived from the middle ring of three concentric cycles of bundles in the young stem, while traces from the innermost "medullary bundles" supply the axillary branches (Pant & Mehra, 1961). The bundles of the outer ring become connected by an interfascicular cambium that initiates the development of up to 5 or more successive rings of anomalous secondary growth containing distinct collateral bundles embedded in a conjunctive tissue of elongated living cells that become lignified. Successive supernumerary cambia arise in the outer parenchyma cells of the phloem produced outwardly by the previous cambium (Maheshwari, 1930; Esau, 1965).

Floral ontogeny is acropetal in sequence, with no evidence of a second perianth whorl in either *B. diffusa* or *B. repanda* (Joshi & Rao, 1934). A single carpel arises from one side of the base of a terminal nucellus and gradually incloses it. Development of the male and female gametophytes is normal, and embryo development is of the Capsella type (Bhargava, 1932; Maheshwari, 1929). The scanty endosperm, which is initially nuclear in its development, is used up in the development of the embryo, leaving a substantial central column of whitish mealy perisperm (nucellar tissue) as a reserve food for the embryo (Bhargava, 1932; Maheshwari, 1929). The five-ribbed perianth of *B. diffusa* is supplied by one cycle of five traces, while the ten-ribbed perianth of *B. repanda* receives ten traces derived as two pentamerous cycles from the pedicellar stele (Joshi & Rao, 1934).

Betacyanin pigments have been demonstrated in five species of *Boerhavia* (*B. coccinea, B. erecta, B. intermedia, B. scandens, B. spicata*), as well as in *Anulocaulis gypsogenus* and *Cyphomeris gypsophiloides* (Wohlpart & Mabry, 1968). The reported presence of the alkaloid punarnavine in *B. diffusa* L. has been proven incorrect (Sircar, 1944). Raphides of calcium oxalate are extremely abundant in leaves, floral parts, and fruits of *Boerhavia.* When immersed in water the accrescent perianth base of *B. erecta* develops along the ribs extensive swellings of whitish slime, the significance of which is not known (Heimerl, 1889).

Boerhavia is of no economic significance, but various species are used locally in folk-medicine, as food, or as fodder. Roots of *B. diffusa* (syn. *B. repens*) are eaten by natives in Australia and used as a purgative, anthelmintic, or febrifuge in Malaysia. Leaves of *B. diffusa* are used as a pot-herb or in soups, or a liquid extract of them may be used for asthma and jaundice, or as a diuretic, emetic, or expectorant. Roots of *B. tuberosa* Lam. are eaten by natives in Peru, and plants of *B. pentandra* are grazed by livestock in South Africa (Cooke, 1910; Stemmerik, 1964; Uphof, 1968).

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Tribe PISONIEAE Meissner

4. **Pisonia** Linnaeus, Sp. Pl. 2: 1026, 1027. 1753; Gen. Pl. ed. 5. 451. 1754.

Dioecious [or monoecious] trees, erect to lax or scandent shrubs, or scrambling woody vines; stems armed or unarmed; lateral branches some-

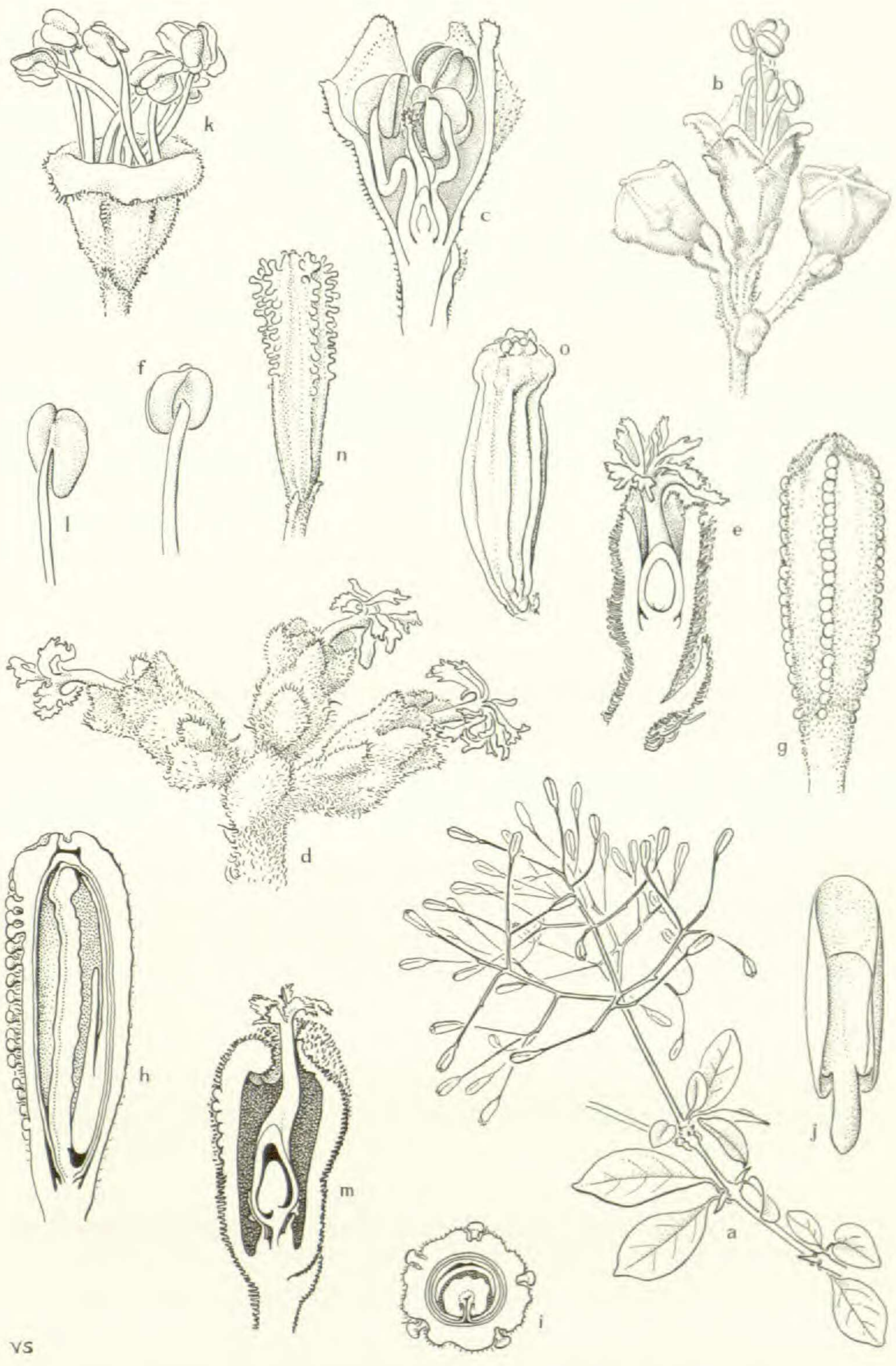

FIGURE 4. **Pisonia.** a–j, *P. aculeata*: a, branch with young fruit, one inflorescence removed, × 1/2; b, cluster of staminate flowers, × 6; c, staminate flower in vertical section, × 12; d, cluster of carpellate flowers, × 12; e, carpellate flower in partial section, the funiculus not visible behind ovule, × 15; f, stamen, × 12; g, mature accessory fruit (accrescent calyx base inclosing fruit), × 5; h, same, in section to show fruit with single seed, embryo with endosperm (flat stipple), × 6; i, same in cross section, the embryo cut through cotyledons, endosperm white stipple on black, × 6; j, embryo — note unequal cotyledons, × 6. k–n, *P. rotundata*: k, staminate flower, × 8; l, stamen, × 12; m, carpellate flower in partial section — note staminodia, × 15; n, mature accessory fruit, × 5. o, *P. floridana*: mature accessory fruit, × 5.

times short, stout, rigid and spine-like, terminating in a short, curved spine; axillary buds sometimes modified as a short recurved thorn, with accessory buds producing lateral growth from the axil. Leaves opposite to subopposite [or alternate], simple, entire, exstipulate, petiolate, glabrous or pubescent, more or less coriaceous. Inflorescence terminal or lateral, diffuse to congested, umbelliform to corymbosely thyrsiform pedunculate cymes. Flowers small, imperfect [or perfect], subtended by 1–3 small, subverticillate to verticillate bracteoles, sessile or pedicellate; perianth more or less fleshy, purple or reddish to yellowish green or greenish white. Staminate perianth ± obconic-campanulate, the limb 5-dentate, with short teeth, aestivation induplicate-valvate; stamens 6–10 [or up to 40], exserted [or included], filaments filiform, unequal, basally connate [or free]; anthers oblong or didymous, basifixed or dorsifixed; pollen tricolpate [6- or 12-rugate]; reduced sterile ovary present. Carpellate perianth tubular, narrowly campanulate to urceolate, the limb short, erect or spreading, 5 (–10)-toothed, persistent; staminodes about as long as the ovary, with rudimentary anthers, or reduced in varying degree to a low, occasionally glandular-dentate disc adnate to the stipe of the carpel; gynoecium a solitary carpel; ovary superior, sessile or stipitate; style terete, elongate, slightly exceeding the perianth; stigma penicillate [to capitate], persistent; ovule solitary, basal, anacampylotropous; integuments two, the outer forming the micropyle. Accrescent calyx glabrous or pubescent, fleshy to coriaceous, terete or angular, eglandular or glandular, the viscid capitate glands subsessile to shortly stipitate, uniseriate to biseriate on (or in costae along) the angles, the stalk of glands whitish to blackish, the head usually blackish. Fruit an elongate, membranaceous or coriaceous utricle enclosed within the persistent calyx. Seed with a deep longitudinal furrow; seed coat translucent, adhering to the pericarp. Embryo straight, the short radicle inferior; cotyledons broad, involute, surrounding the scanty, gelatinous endosperm and abundant mealy perisperm. (*Guapira* Aublet, *Pallavia* Vell., *Torrubia* Vell.) TYPE SPECIES: *P. aculeata* L. (Named in commemoration of William Piso, 1611–1678, a Dutch physician and naturalist who travelled in Brazil.) — Pisonia, blolly.

A large and variable genus of perhaps 35–75 species distributed in the tropics and subtropics of the World. The genus has its primary center of development and distribution in the West Indies, Central America, and South America, and a secondary center in the southwest Pacific, with about eight species occurring in Malaysia (two of these extending to Australia and New Zealand) and about five species endemic to Melanesia and Polynesia. Three of the Malaysian species also reach Madagascar and Africa (Stemmerik, 1964a). About six species of the genus have been recognized in our area in coastal southeastern Florida and the Florida Keys, and one of these (*P. aculeata*) also occurs in Texas.

Two of our species belong to section PISONIA (sect. *Glanduliferae* of Heimerl 1889, 1934), which is characterized by Stemmerik (1964b) as having "prickles [stipitate glands] on the anthocarp, no rostrum [elongate sterile apex of the accrescent calyx]. Stamens 6–10." The pantropical *Pisonia aculeata*, cock-spur, devil's-claws, pull-and-hold-back, old-hook, occurs on sea beaches, and in hammocks of southern peninsular Florida and the Keys as a thorny, densely branched scrambling vine with greenish-yellow or purple (?) calyx, and small, slender longitudinally 5-angled clavate fruits bearing a single row of low, blackish (in herbarium specimens) stipitate glands along the length of each angle, and 6–8 stamens in the staminate flowers. The species ranges from southern Texas, Florida, and the West Indies southward to tropical South America in the New World.

A single collection of a plant possibly referable to *Pisonia aculeata* var. *macranthocarpa* Donn. Sm. (*Pisonia macranthocarpa* Donn. Sm.) collected in 1881 by A. H. Curtis, is in the Arnold Arboretum herbarium. In a field note attached to the sheet Curtis states "A *Pisonia* found in hammock W. of Bay Biscayne. Except for the fr. I would have called it *P. aculeata* — tall-climbing like the latter & just as prickly." The mature dried fruits are 16–17 mm. long and 4–5 mm. wide and are more or less elliptic-oblong, bearing along the length of the angles of the calyx base five rows of stout uniseriate to biseriate whitish stipitate glands up to 1 mm. long, with small blackish heads. *Pisonia aculeata* var. *macranthocarpa* is otherwise known from Cuba and Central America to Venezuela.

Pisonia rotundata Griseb. (*P. subcordata* var. *rotundata* of Heimerl, *Torrubia rotundata* (Griseb.) Sudw.) is a low spreading shrub or small tree with broadly elliptic or ovate to obovate, pubescent, leathery leaves, with the veins strongly raised on the lower surface, dense cymes of greenish to whitish flowers, and small broadly to narrowly obovoid fruits about 5–7 mm. long bearing 5 rows of uniseriate stipitate glands along the angles of the distal third (or half) of the accessory fruit. The species is known from the Florida Keys, the Bahamas, Puerto Rico, Cuba, and the Isle of Pines.

The remaining species of our area differ from those of sect. PISONIA in having eglandular, fleshy, reddish [to black], drupe-like calyx bases. These were placed by Heimerl (1889, 1934) in his sect. EUPISONIA, but were transferred to *Torrubia* Vell. by Britton (1904), and later to *Guapira* Aublet (Little 1968; Lundell, 1968). Stemmerik (1964b) did not consider this group of species, and a formal category (section) apparently does not now exist for them within the genus *Pisonia*. Two taxa from our area, originally described as species of *Torrubia* (*T. Bracei* Britton, *T. globosa* Small), and recently transferred to *Guapira*, have never appeared under the name *Pisonia*. They are poorly represented in our collections, and their systematic position remains problematical. They are cited here as species of *Guapira*.

The well known *Pisonia discolor* Sprengel var. *longifolia* Heimerl (*P. longifolia* (Heimerl) Sargent, *Torrubia longifolia* (Heimerl) Britton, *Guapira longifolia* (Heimerl) Little), commonly called the beef-tree, beef-wood, pork-wood, pigeon-wood, or long-leaf blolly, is a tree 5–15 m. in height, with obovate-oblong leaves broadest above the middle, greenish-yellow imperfect (or perfect?) flowers that appear in autumn, and pink to red or magenta obovoid fruits that are rounded to slightly depressed at the apex, and become obviously ribbed on drying. The variety is found in Florida in dune-scrub, along the shores of salt-water lagoons, and in pinelands and woods from Cape Canaveral to the southern Keys, where

FIGURE 5. **Pisonia.** a–l, *P. discolor* var. *longifolia* (*Guapira longifolia*): a, staminate flowers, × 8; b, staminate flower in vertical section, × 12; c, stamen, × 15; d, carpellate inflorescence, × 2; e, carpellate flowers, × 12; f, carpellate flower in vertical section — note staminodia and penicillate stigma, × 20; g, infructescence, accrescent calyx bases berry-like and glabrous, × 1; h, mature accessory fruit in vertical section to show single seed — note parts of two unequal cotyledons on each side, surrounding perisperm (stippled), × 6; i, same, in cross section, embryo cut through cotyledons and hypocotyl, perisperm stippled — note longitudinal groove formed by intrusion of seed coat, × 6; j, fruit in cross section above epicotyl to show unequal cotyledons surrounding perisperm, seed coat intruding into perisperm, × 6; k, embryo, dorsal view, to show basal lobes of outer, larger cotyledon covering hypocotyl, × 6; l, same, side view, × 6.

the largest specimens were reported (Sargent, 1905) to occur on Elliot's Key and Old Rhodes Key. It is also common in the West Indies and ranges southward to Brazil. The typical *P. discolor* var. *discolor*, with leaves ovate to lance-ovate, broadest at or below the middle, is less well represented in our area, occuring in hammocks and thickets principally along the east coast of southern Florida. *Guapira globosa* (Small) Little (*Torrubia globosa* Small), the roundleaf blolly, is a small tree with small orbicular-cuneate to suborbicular leaves 1–2 cm. long, greenish-purple flowers, and subglobose juicy dark-red fruits. It is reported in hammocks of southeastern coastal Florida and the Keys. *Guapira Bracei* (Britton) Little (*Torrubia Bracei* Britton) is a gray-barked shrub or small tree with obovate leaves that are broadest above the middle and cuneately narrowed at the base, purplish flowers, and red, oblong-obovoid, apically truncate fruits about twice as long (7–8 mm.) as broad. The species was described from the Bahamas and is reported to occur in hammocks and adjacent pinelands on the lower eastern coast of peninsular Florida and in the Keys. *Pisonia floridana* Britton in Small (*Torrubia floridana* (Britton) Britton, *Guapira floridana* (Britton) Lundell) was described from incomplete material collected only once over a century ago on Rock Key near Key West. Its spatulate to obovate leaves are 2–3.5 cm. long and are supposedly distinctive in their dense puberulence.

In the late nineteenth century many specimens of this group of species from our area were incorrectly referred to *Pisonia obtusata* Swartz (Chapman, 1860, 1897; Heimerl, 1896; Sargent, 1894, Small, 1903). Britton (1904), however, established *P. obtusata* Sw. as a synonym of the West Indian and South American *P. inermis* Jacq. (*Torrubia inermis* (Jacq.) Britton) and assigned the Floridian specimens to his *Torrubia longifolia* (Heimerl) Britton. Heimerl (1896) recognized some specimens of our area only as varieties of West Indian species (*P. discolor* Sprengel var. *longifolia* Heimerl, *P. subcordata* Sw. var. *rotundata* (Griseb.) Heimerl).

More recently the material of *Pisonia* from our area has been studied by R. W. Long (Long & Lakela, 1971), who considers the various and intergrading eglandular forms in Florida to represent only phases of the West Indian *P. discolor* Sprengel. He recognizes two varieties in our area: var. *discolor*, with ovate, oval or lance-ovate leaf blades broadest at or about the middle, and *P. discolor* var. *longifolia* Heimerl (incl. *T. Bracei* Britton, *G. Bracei* (Britton) Little, *T. globosa* Small, *G. globosa* (Small) Little, *T. longifolia* (Heimerl) Britton) with leaf blades obovate or oblanceolate to narrowly spatulate, broadest above the middle.

Very few herbarium specimens bear field notes of any kind regarding plant size, habit, bark or wood form and color, flower color or odor, pollinators, fruit dispersal, etc. There are apparently no chromosome counts for the species of our area and possibly none for the genus. A modern monographic study of this genus, defining generic as well as specific boundaries, is badly needed.

The floral ontogeny and embryology of *Pisonia aculeata* have been briefly described by Venkateswarlu. He found floral organogeny to be acropetal in sequence. Embryological details include the presence of a secretory tapetum in the anthers; tricolpate pollen grains that are trinucleate when shed; the formation of an obturator-like structure in the ovary; formation of a nucellar cap; Polygonum-type embryo-sac development; nuclear endosperm; and an Asterad type of embryogeny. The woods of the genus are notable chiefly for their anomalous secondary growth in the form of successive rings of vascular bundles (Metcalfe & Chalk).

In the Pacific region the sticky-viscid fruits of *Pisonia grandis* R. Br. and *P. umbellifera* (Forster) Seem. are noted for catching insects, small lizards, and birds. Fruits or inflorescences of these species are hung as fly-catchers. Birds disseminate the sticky fruits, but excessive accumulation of fruits on the bodies of small birds may render them incapable of flight and cause their eventual death (St. John, Stemmerik, White, Govett, Kirk). Airy Shaw speculates that the unusual distribution of *P. grandis*, which is largely confined to small, often uninhabited "bird islands," may be partly linked to a need for a supply of bird-guano in association with a coral or limestone substrate for its germination and early development.

The generic limits of *Pisonia* are not clear. The genus has been considered on a world-wide basis only by Heimerl. His concept of the over-all limits of the genus changed over the years, as evidenced by his later recognition or acceptance of segregate genera, but he consistently maintained a broader view of *Pisonia* proper than most regional workers by retaining both glandular- and eglandular-fruited species within the genus. In his earlier papers (1889, 1897) he reduced several genera of previous authors either to sectional rank or to synonymy and recognized six sections in the genus. He revised the species of the two sections occuring in our area in 1896. Britton (1904) disagreed with Heimerl's concept of the genus, and segregated as the genus *Torrubia* the Floridian and West Indian species with unarmed stems and eglandular, red drupe-like calyx bases while maintaining in *Pisonia* the armed, glanduliferous, and coriaceous-fruited species typified by *P. aculeata*. The segregation of *Torrubia* was accepted by Standley (1911), and later by Small (1933), who had earlier (1903) recognized only *Pisonia* in the southeastern United States. Standley (1911) also elevated Heimerl's sect. PISONIELLA to generic rank, and later (1918) re-established sect. CEPHALOTOMANDRA at the generic level. In 1934, Heimerl recognized only two sections in *Pisonia* (GLANDULIFERAE and EUPISONIEAE), which he considered to differ only in the presence or absence of glands on the calyx tube. The other four sections of his earlier treatments were established as segregate genera, including *Pisoniella* (Heimerl) Standl., *Calpidia* du Petit Thouars (*Pisonia* sects. *Timeroya* and *Prismatocarpae* of Heimerl, 1889), *Rockia* Heimerl (*Pisonia sandwicensis* Hillebr.), and *Cephalotomandra* Karsten & Triana (*Pisonia* sect. *Cephalotomandra* of Heimerl, 1889).

Woodson & Schery (1961) revived the earlier name *Guapira*, which had been established as a synonym of *Pisonia* by Hallier (1918), to replace *Torrubia* as the generic name for the fleshy-fruited eglandular species.

The name *Torrubia* was then proposed for conservation over *Guapira* (Little, 1964) but was rejected (McVaugh, 1968). Consequently a large number of new combinations have been made in *Guapira* (Lundell, 1968; Little, 1968).

Stemmerik (1964a, b) revised the Old World species of *Pisonia*, but did not consider the New World species. He again reduced the segregate genera *Calpidia*, *Heimerliodendron* Skottsb. (*Heimerlia* Skottsb.), and *Rockia* to synonymy under *Pisonia*, and tentatively proposed for the Pacific species four sections based on the presence or absence of stipitate glands and of a rostrum on the calyx tube, and on the number of stamens in the flowers, but stated that, except for historical precedent, he probably would not have proposed such subdivisions.

Meissner (1841) established a tribe Pisonieae, including the genera *Neea* Ruiz & Pavón, *Pisonia*, *Reichenbachia* Sprengel, and *Salpianthus* Humb. & Bonpl. Choisy, in DeCandolle's *Prodromus*, placed *Pisonia* in his suborder (subfamily) Boerhavieae, and separated the known species into two groups, those with stems armed (incl. *P. aculeata* L.) and those with stems unarmed. The species of the latter group were then divided on a geographical basis. Bentham & Hooker (1883) recognized a tribe Pisonieae in which they included *Pisonia*, *Timeroya* Montrousier and *Cephalotomandra* Karsten & Triana (both subsequently reduced by Heimerl to sections under *Pisonia*), and the closely related *Neea* Ruiz & Pavón (which had been included in *Pisonia* by Baillon, 1872). The tribe has been maintained in subsequent major treatments of the family (Heimerl, 1889, 1896, 1897, 1934; Eckardt, 1964).

Berry described fossil material of *Pisonia* (*P. apalachicolensis* Berry), probably dating from the end of the Oligocene, from the Alum Bluff Formation in Liberty County, Florida, stating that about fifteen fossil species of the genus have been described, the earliest being from the Upper Cretaceous of both America and Europe.

The genus is of little economic significance. Branches of *P. aculeata* are reported to be used as barrel hoops in Jamaica, and a decoction of its leaves is used against rheumatic and venereal disease in Jamaica and Yucatán. A decoction of the fruits of *P. capitata* (S. Watson) Standley is used against fevers by certain Indians in Mexico. The wood of *Pisonia Zapallo* Griseb., of Argentina, is strong enough to be used in box-making and for general building construction. The light-yellowish, chlorotic leaves of a cultivated race of *P. grandis* are boiled and eaten as a pot-herb in Malaysia, where the trees are known as "Mollucan cabbage," "cabbage-tree," or "lettuce-tree" (Airy Shaw, Stemmerik, Uphof). The leaves of *P. umbellifera* (*P. Brunoniana*) Endl. are used as a diuretic and the roots as a purgative in the Pacific Islands (Uphof).

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DEPARTMENT OF BOTANY
UNIVERSITY OF NEW HAMPSHIRE
DURHAM, NEW HAMPSHIRE 03824